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Combining taxon-by-trait and taxon-by-site matrices for analysing trait patterns of macroinvertebrate communities: a rejoinder to Monaghan & Soares (2014)

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Running head: How to combine taxa-by-trait and taxa-by-site matrices?

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Summary

1. Monaghan & Soares (2014) suggested that combining traits with log-transformed abundance of taxa may cause anomalies in analyses of stream macroinvertebrate communities. While they addressed an important issue in stream ecology, here we present an opposite view. To identify the causes of these contrasting opinions, we carefully examined the examples provided by Monaghan & Soares (2014) and demonstrated how traits can be weighted by the presence, abundance and log-transformed abundance of the taxa in a meaningful way.
2. We found that Monaghan & Soares (2014), following other authors, use the term 'weighting' differently from classical papers of stream ecology. The general practice is to calculate the sum of trait values multiplied by the abundance of each taxon and divide it by the total invertebrate abundance to get a community-level trait value. In contrast, Monaghan & Soares (2014) did not perform the final division and consequently did not get a standardized community-level trait value. It follows that the term "weighting" is used with different meanings in stream ecology, and ecologists should keep these differences in mind.
3. We agree with Monaghan & Soares (2014) that the addition of log-transformed data is equivalent to multiplication on an arithmetic scale. However, we disagree that this provides an inconsistent scaling that confounds quantitative analyses. Using example data sets, we illustrate how trait-based data analysis can be preformed in community ecology in a meaningful way.

Introduction

In a recent paper, Heino, Schmera & Erős (2013) provided an overview of trait patterns of stream communities from a macroecological perspective. In this paper, reference was made to Gayraud *et al*. (2003), who showed that abundance-weighted traits were less powerful than presence-absence weighted traits in discriminating communities under different degrees of human impacts, and to Statzner & Beche (2010), who therefore advocated the use of the second type of weighting for practical biomonitoring due to logistic constrains (e.g. sorting of qualitative samples makes

assessment programmes more cost effective). Heino *et al*. (2013) pointed out that these findings contradict the results of taxon-based analyses which suggest that, if taxa are weighted by their abundance, then communities are better separated in relation to environmental variation than when taxa are weighted only by their presence. Based on an overview of the literature, Heino *et al*. (2013) concluded that results of presence- and abundance-based analyses should be evaluated carefully when examining traits of organisms, because differences among studies can reflect both methodological (i.e. handling of data) and real ecological differences (see p. 1549 in Heino *et al*., 2013). More recently, Monaghan & Soares (2014) stated that (1) Heino *et al*. (2013) identified the weak explanatory power of abundance data as a major limitation of macroinvertebrate trait analysis and that (2) the log-transformation of abundance data may cause anomalies in trait-based analyses. We disagree with both conclusions, because (1) Heino *et al*. (2013) did not actually state this (see above) and because (2), in our view, log-transformation of abundance data in trait-based analyses can also be meaningful. To reveal the causes of these differing views, we go through the examples provided by Monaghan & Soares (2014) and examine how traits can be weighted by the presence, abundance and log-transformed abundance of the taxa. To do this, first we define the terminology used here, comment on the approach of Monaghan & Soares (2014) and show how this procedure should be performed.

Terminology

Characterizing taxa by their traits is a challenging task in ecology. A research team (Stazner *et al*., 1994) studying the Upper Rhone River in France made a seminal contribution by determining which traits can be used and how to examine macroinvertebrate communities from a 'functional' perspective. High heterogeneity of organisms, remarkable variation within taxa, gaps and uncertainties in our knowledge led them to adopt a "*fuzzy coding"* system (Chevenet *et al*., 1994). Fuzzy coding is based on expert opinion and assigns an integer score, ranging from 0 (no affinity) to an arbitrary maximum, often 5 (high affinity), to express the relationship of a taxon to a particular trait. To improve comparability, scores are often

standardized by the total number of scores within a taxon (Usseglio-Polatera *et al*., 2000, Bady *et al*., 2005, Dolédec *et al*., 2006).

Information on taxa characterized by different traits can be summarized by a taxon-by-trait matrix (**A**) of size s × t, in which rows represent taxa and columns correspond to traits describing a well-defined character (e.g. the feeding habit) of macroinvertebrates. More formally,

$$\mathbf{A}=\begin{bmatrix} a_{11} & a_{12} & & a_{1t} \\ a_{21} & a_{22} & & a_{2t} \\ & & a_{ij} & \\ a_{s1} & a_{s2} & & a_{st} \end{bmatrix}$$

Each entry in the matrix (a_{ij}) is determined such that $\sum_{j=1}^{t} a_{ij} = 1$ for every row i (see Bady *et al*., 2005). In a sense, the a_{ij} values express the relative importance of trait j for taxon i or, in other words, the relative affinity of taxon i to trait j. For example, if a given taxon acts exclusively as a shredder, it cannot be a predator or anything else: only one value can be 1, and all the others are zero (see also Chevenet *et al*., 1994; Dolédec *et al*., 2006). Other possibilities, with $0 < a_{ij} < 1$ are shown in the upper part of Table 2 of Monaghan & Soares (2014). Note, however, that zero values are missing from that matrix, which takes a mathematically correct form as given below:

$$\mathbf{A}=\begin{bmatrix} 0.17 & 0 & 0.5 & 0.33 & 0 \\ 0 & 0.75 & 0.25 & 0 & 0 \\ 0 & 0.2 & 0 & 0.2 & 0.6 \\ 0 & 0.5 & 0 & 0 & 0.5 \\ 0 & 0.4 & 0.6 & 0 & 0 \\ 0 & 0 & 0 & 0.75 & 0.25 \\ 0.25 & 0 & 0.75 & 0 & 0 \end{bmatrix}$$

Sampling sites characterized by different taxa can be summarized by a taxon-by-site matrix (**B**) of size s × z, in which rows represent taxa, and the columns correspond to sampling sites. Each entry b_{ik} in **B** is the abundance of taxon i at site k:

$$\mathbf{B} = \begin{bmatrix} b_{11} & b_{12} & & b_{1z} \\ b_{21} & b_{22} & & b_{2z} \\ & & b_{jk} & \\ b_{s1} & b_{s2} & & b_{sz} \end{bmatrix}$$

The top left part of Table 2 in Monaghan & Soares (2014) displays such a matrix for seven taxa and a single site, so it is in fact a column vector, abbreviated as **b**:

$$\mathbf{b} = \begin{bmatrix} 80 \\ 50 \\ 100 \\ 20 \\ 40 \\ 30 \\ 20 \end{bmatrix}$$

Comments on the approach of Monaghan & Soares (2014)

Monaghan & Soares (2014) write that, if standardized trait values are used "as a non-linear weighting for trait descriptions", then the "practitioners should be aware of the potential of inconsistent weighting". This causes some uncertainty, because the term 'weighting' in Monaghan `& Soares (2014) is different from that used by Charvet *et al*. (2000) and Statzner *et al*. (2001). Charvet *et al*. (2000) and Statzner *et al*. (2001) summed the trait values multiplied by the abundance of each taxon and divided by the total invertebrate abundance to get a community-level trait value. In contrast, Monaghan & Soares (2014), following Archaimbault *et al*. (2005) and Larsen & Ormerod (2010), did not perform the final division, only summed the trait values multiplied by the abundance of each taxon. In other words, some studies weight by proportions, whereas others by abundance. It follows that the term "weighting" has been used with at least by two different meanings in stream ecology. Although the proper measurement of the overall community trait values is still debated (Ricotta & Moretti, 2011), we argue that, from a statistical point of view, *weighting* means that

147 some elements have more impact on the result than other elements in the same set.
148 Stream ecologists should be aware of these two variants when comparing different
149 results.
150
151 Monaghan & Soares (2014) exemplify this inconsistent weighing by back-
152 transformation, and emphasise that the "addition of log-transformed data is equivalent
153 to multiplication on an arithmetic scale" (point 2 in their Summary). From a
154 mathematical point of view we agree, but note that accepting this point would exclude
155 all kinds of nonlinear transformations (square-root, logarithmic, etc.) from the toolkit
156 of statistical data analysis. Nonlinear transformations modify the original data
157 structure in a meaningful way and, if properly used, facilitate significance tests by
158 decreasing skewness in the data (Elliot, 1977; Podani, 2000; Legendre & Legendre,
159 2012). Furthermore, community ecologists very often use log transformation for
160 'equalization' purposes, that is, to balance the importance of variables (species, or
161 other taxa) before cluster analysis or ordination. The result of this operation is that
162 species with highly unequal abundance will be almost equally influential in
163 multivariate analysis. Non-linear transformation can be conceived as a parameterized
164 series, with raw abundances at one end and presence-absence data at the other (e.g.,
165 Clymo transformation, see Podani, 2000). In any case, it is fundamental that all data
166 are transformed by the same method *before* any other calculations are performed.
167 Since the scale of data (i.e. linear vs. nonlinear) is selected completely arbitrarily by
168 the investigator (pH is measured mostly at a nonlinear scale, while individuals are
169 counted mostly at a linear scale), changing from a linear to a nonlinear scale, or *vice*
170 *versa*, is acceptable. Finally, we do not know of any situation when back-
171 transformation to the original scores would be necessary, so that the warning by
172 Monaghan & Soares (2014) is mainly of academic significance.
173
174
175 **Combining traits with the abundance of a single taxon**
176
177 Monaghan & Soares (2014) state that "the abundance of taxa represented by
178 respective trait classes is obtained by multiplying the total abundance by the
179 proportionate frequencies of the traits". Moreover, their Table 1 exemplifies the
180 situation and shows how this procedure runs with the feeding habits of larvae of the

trichopteran *Psychomyia* using raw abundance and standardized trait values (Table 1a of Monaghan & Soares, 2014), using the log-transformation of the product (their Table 1b,c), and using the log-transformed abundance multiplied by the standardized trait values (their Table 1d). However, Monaghan & Soares (2014) give no information about the purpose of these calculations.

Basically, this table is unnecessary because the utility and the effects of log transformation of community data is only apparent when several species appear in the data simultaneously. For a single species, we cannot see why these operations are important. Multiplying a standardized trait value by the raw abundance of that single species: (a) may be correct but not useful, because the standardized trait values of a species provide sufficient information about the (feeding habits of the) taxon anyway. Operations (b-c) are illogical (but are in fact identical) because the raw abundances are multiplied first by the relative frequency of the trait while log transformation is undertaken only subsequently. As mentioned previously, handling the data this way is not correct, because transformation should be done first in order to ensure consistency in subsequent analyses of the data.

Combining traits with the abundance of several taxa in a community

In examining communities, Monaghan & Soares (2014) suggest that "the relative abundance of trait classes at assemblage level is given by the sum of the trait frequencies of respective taxa. This can be calculated by multiplying the respective taxon abundances by their corresponding proportionate frequencies, followed by the summation of the resultant trait abundances" and exemplify this and some log-transformed versions in their Table 2. They write in their Summary that, compared to other versions, the summation of the product of log-transformed abundance and standardized trait values "represents a non-linear abundance weighting of trait frequencies, as opposed to an expression of trait abundance *per se*, because the addition of logarithmic data is equivalent to multiplication on an arithmetic scale, summing this abundance-weighted frequencies provides an inconsistent scaling of trait abundance that might confound quantitative comparison" .

214 This also risks confusion because Monaghan & Soares (2014) use the term "*relative*
215 abundance of trait classes at assemblage level" (italics ours) to specify the trait value
216 of the community (*community traits* in Heino *et al*., 2013). It is not clear why is this
217 “relative”, which generally means a comparison to some standard (or total). Another
218 source of confusion, compared to the methodology of Charvet *et al*. (2000) and
219 Statzner *et al*. (2000), is that the "relative abundance of trait classes at the assemblage
220 level" is the sum of products ("This can only be calculated by multiplying the
221 respective taxon abundances by their corresponding proportionate frequencies,
222 followed by the summation of the resultant trait abundances") without dividing by the
223 total abundance of invertebrates. In the following, we show how to combine
224 standardized trait values of several taxa in a community to calculate community-level
225 trait values, where weighting includes a division.
226
227 Let us start with the taxa-by-traits and taxa-by-sites matrices provided in Table 2 of
228 Monaghan & Soares (2014) and, for the time being, focus only on the
229 presence/absence of the taxa and on the trait "fine sediments". The data suggest that
230 *Psychomyia* has a standardized trait value of 0.17 and *Agapetus* a value of 0.25. We
231 should not forget, however, that the other five taxa (*Sericostoma*, *Polycentropus*,
232 *Odontocerum*, *Drusus* and *Hydropsyche*) have a standardized trait value of 0 (no
233 affinity for feeding on fine sediment). It follows that our community contains five
234 taxa with a standardized trait value of 0, one taxon (*Psychomyia*) with a standardized
235 trait value of 0.17 and one (*Agapetus*) with a value of 0.25. We can illustrate this on a
236 frequency histogram where the horizontal axis shows the standardized trait values
237 while the vertical axis corresponds to their frequencies (top-left subplot in Fig. 1). The
238 mean of these values gives the community trait value (indicated by the arrow). How
239 can we interpret this value? It tells us that if we consider only the presence of the taxa
240 then the community is represented by an average value of 0.06 (= [0.17 + 0.25 + 5 x
241 0]/7) with respect to the trait ‘feeding on fine sediment’. In other words, members of
242 the community, based on the presence of taxa, have a low affinity for feeding on fine
243 sediment. It follows that weighting by the presence of taxa means that we give more
244 importance to those elements of the set (to those standardized trait values of the
245 observed trait values), which are most frequently represented by the taxa in the
246 community. Examining the issue from a taxonomic point of view, we give equal
247 importance to each taxon. We can do the same procedure for the other traits (top row

248 in Fig. 1). We should note that it is really beneficial that our calculation is based on
249 standardized trait values, because the sum of community trait values equals 1. It
250 follows that we can clearly interpret which function is the most characteristic of the
251 community (in this case, feeding as a scraper).
252
253 The logic of using abundances is similar to that used for presence: we count the
254 frequencies of standardized trait values and use these frequencies to calculate
255 community trait values. However, compared to using the *presence of the taxa*, here
256 we use the numerical abundance of *individuals* to weight the standardized trait values.
257 In other words, we have 240 individuals (50 *Sericostoma*, 100 *Polycentropus*, 20
258 *Odontocerum*, 40 *Drusus* and 30 *Hydropsyche*) showing the standardized trait value 0
259 for fine sediment trait, we have 80 individuals (80 *Psychomyia*) showing the
260 standardized trait value 0.17 and, finally we have 20 individuals (20 *Agapetus*) with a
261 standardized trait value 0.25 (bottom-left subplot in Fig. 1). The community trait
262 value is the weighted average of these values, and the measure is usually known as
263 community-weighted mean trait value (Ricotta & Moretti, 2011). In the example,
264 (80x0.17 + 20x0.25 + 240x0)/340 = 0.055. For the other four traits we obtain 0.245,
265 0.269, 0.202 and 0.228. We should note that the sum of these community trait values
266 is 1 and that the community trait value corresponds to the mean standardized trait
267 value of an *individual* in the community. The latter calculations (without the final
268 division) are missing from Table 2 of Monaghan & Soares (2014), although the
269 weighted values are presented in row a (for example, 80 x 0.17 + 20 x 0.25 = 18.6).
270
271
272 **Log-transformation of abundance in trait-based community analyses**
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274 What happens if we use the log-transformed abundance for weighting? First, we
275 transform the abundance of each taxon. While the original column vector contains
276 abundances of 80, 50, 100, 20, 40, 30 and 20, the log-transformed column vector
277 contains abundances of ln(80) = 4.38, ln(50) = 3.91, ln(100)= 4.61, ln(20) = 2.99,
278 ln(40) = 3.69, ln(30) = 3.40 and ln(20) = 2.99. Note that, in order to make the example
279 comparable with Monaghan & Soares (2014), we use also $\log_e$ transformation
280 (abbreviated to ln), although we suggest that logarithms to the base of 10 are easier to
281 interpret (see below.) We then use these log-transformed abundances, instead of the

282 original abundances. To calculate the frequency of standardized trait value of 0 for
283 fine sediment, we should sum the frequency of taxa with 0 standardized trait value for
284 fine sediment: ln(50) + ln(100) + ln(20) +ln(40) + ln(30) = 18.6. The transformed
285 abundance of standardized trait value of 0.17 for fine sediment is ln(80)= 4.38.
286 Finally, the transformed abundance of the standardized trait value 0.25 equals ln(20)
287 = 2.99. The community trait value can be calculated by the mean of these values
288 [(18.6 x 0 + 4.38 x 0.17 + 2.99 x 0.25) / (18.6 + 4.38 + 2.99) = 0.057. We can
289 calculate frequencies and community trait values for the other traits in similar manner.
290 We should note that the sum of these community trait values equals to 1 (Fig. 1), as
291 required (see also Usseglio-Polatera *et al*., 2000; Dolédec *et al*., 2006).
292
293 There are, however, some problems with such analyses. First, this transformation is
294 not able to handle 0 abundances (in comparing multiple communities, some species
295 may be absent from several sites) because ln(0) is mathematically not interpretable.
296 Therefore, we suggest the use of the log(x+1) transformation, as used by Statzner *et*
297 *al*. (2001), Gayraud *et al*. (2003), Dolédec *et al*. (2006) and also suggested by
298 Monaghan & Soares (2014). Moreover, although the base of logarithms is again an
299 arbitrary decision, we suggest a $\log_{10}(x+1)$ transformation to facilitate interpretation.
300 To demonstrate this, we start with the same taxon-by-trait matrix discussed before,
301 but our community contains only three taxa: 1000 individuals of *Psychomyia*, 100
302 individuals of *Sericostoma* and 10 individuals of *Polycentropus* (other four taxa are
303 represented by 0 individuals). Here, we do not intend to discuss all details of the
304 analyses, but only emphasize some important differences among different weighting
305 schemes. Regarding the trait 'scraper', we have one taxon (*Polycentropus*) showing a
306 standardized trait value of 0, one showing a value of 0.25 (*Sericostoma*), and one a
307 value of 0.5 (*Psychomyia*). Consequently, the community trait value in presence-
308 weighted analyses equals 0.25 (Fig. 2). In abundance-weighted analyses, however,
309 there are 10 individuals with a standardized trait value of 0 (10 individuals of
310 *Polycentropus*), 100 individuals with a standardized trait value of 0.25 (100
311 individuals of *Sericostoma*) and 1000 individuals with a standardized trait value of 0.5
312 (1000 individuals of *Psychomyia*). The community trait value equals to 0.47, very
313 close to the value of *Psychomyia*, the dominant species in the assemblage. In log-
314 transformed abundance-weighted analyses [using a $\log_{10}(x+1)$ transformation], the
315 standardized trait values 0, 0.25 and 0.5 will be multiplied by $\log_{10}(11)=1.04$,

316 $\log_{10}(101) = 2.00$ and $\log_{10}(1001) = 3.00$, respectively (Fig. 2). We should recognize
317 that the $\log_{10}$-transformed abundance expresses the magnitude of the number of
318 individuals in the decimal system. The community trait value will be lower than
319 above, 0.33, reflecting our decision to give less weight to the most common species. It
320 is interesting to see how the community trait value of the scraper trait increases as we
321 change from presence-weighting, through log-transformed abundance weighting to
322 abundance weighting (Fig. 2). All of these suggest that, although Monaghan & Soares
323 (2014) are right in stating that the addition of log-transformed data is equivalent to
324 multiplication on the arithmetic scale, the interpretation of logarithmic transformation
325 is straightforward. Therefore, in our view, papers using log-transformed abundances
326 in trait-based analyses provide not only a useful indicator of environmental conditions
327 (as acknowledged by Monaghan & Soares, 2014), but also a clear and easily-
328 interpretable mathematical procedure.
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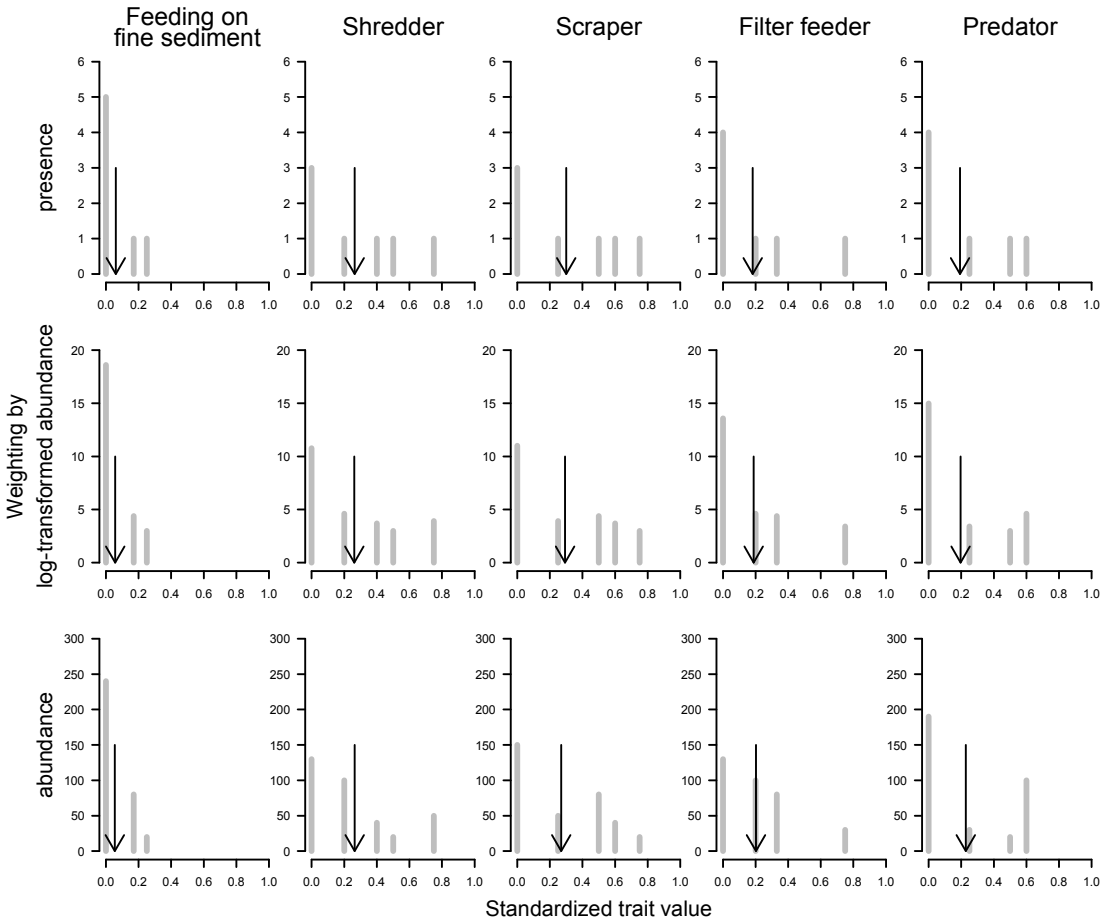

Fig. 1: The frequency distribution of standardized trait values weighted by taxon presence (top row), log-transformed abundance (middle row) and raw abundance (lower row) for five different traits. Grey columns represent frequencies of standardized trait values of the taxa, while arrows show the community-level trait values. The community contains 80 individuals of *Psychomyia*, 50 individuals of *Sericostoma*, 100 individuals of *Polycentropus*, 20 individuals of *Odontocerum*, 40 individuals of *Drusus*, 30 individuals of *Hydropsyche* and 20 individuals of *Agapetus* as displayed in Table 2 of Monaghan & Soares (2014).

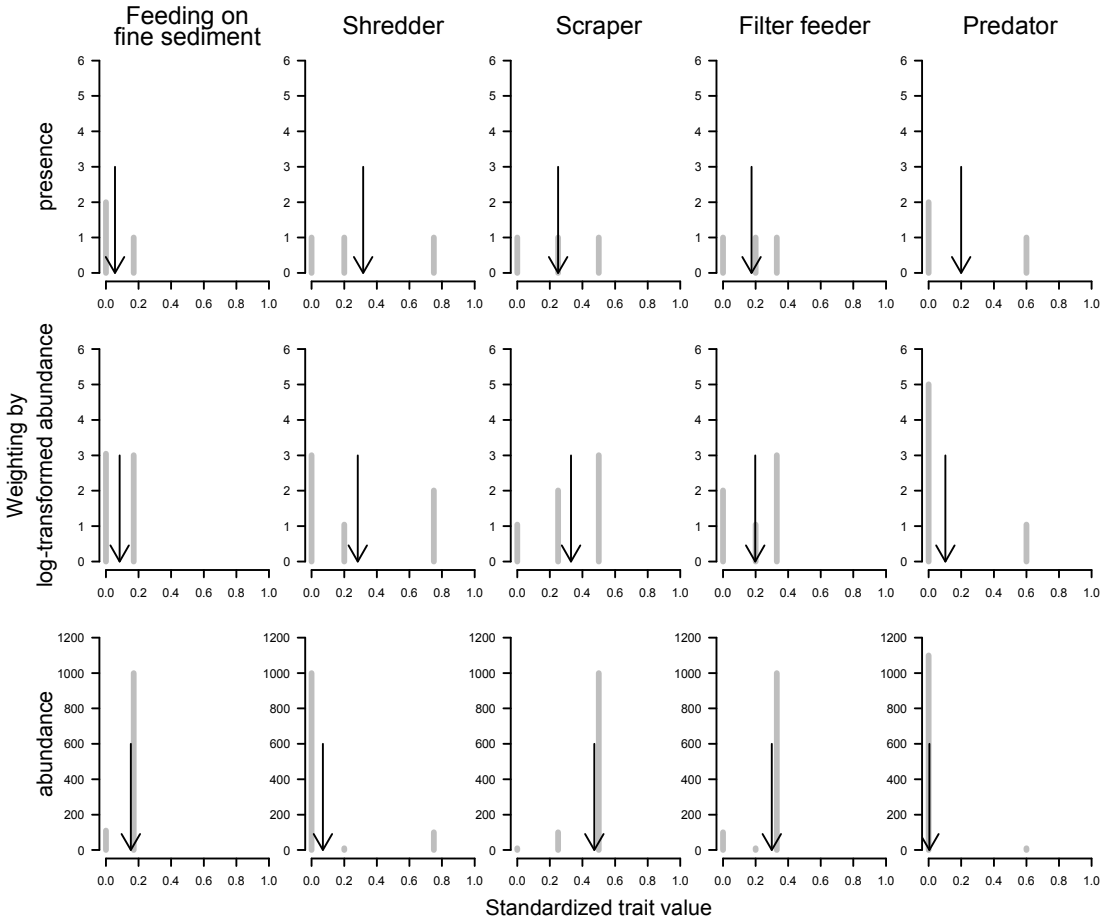

Fig. 2: The frequency distribution of standardized trait values weighted by taxon presence (top row), $\log_{10}$-transformed abundance (middle row) and raw abundance (lower row) for five different traits. Grey columns represent frequencies of standardized trait values of the taxa, while arrows show the community-level trait values. The community contains 1000 individuals of *Psychomyia*, 100 individuals of *Sericostoma* and 10 individuals of *Polycentropus*.